LEAVES OF THE HELOBIEAE[1]

AGNES ARBER

(WITH PLATE I)

Introduction

In a paper published in 1918 (1), the phyllode theory of the monocotyledonous leaf was discussed in general terms, and in subsequent articles in this and other journals (2, 3, 4, 5) attempts have been made to trace the results of applying this theory in various special cases. In the present paper, it is proposed to study the leaves of the Helobieae, to see how far the phyllode theory will help toward interpreting them. I am indebted for material to Professor OSTENFELD of Copenhagen; to the Director of the Royal Botanic Gardens, Kew; to the Keeper of the Department of Botany, British Museum (Natural History); and to the Superintendent of the Cambridge Botanic Garden.

The Helobieae of ENGLER consist of seven families of water or marsh plants. Their common characters are difficult to define, but they are united by a macropodous embryo, and on the whole they appear to form a fairly coherent group. The seven families will be considered individually, and then the general conclusions drawn. Since I believe that the Alismaceae and their allies include the less specialized types within the cohort, these families will be discussed first, instead of following ENGLER's sequence.

Alismaceae

The literature on the protean leaf forms of the Alismaceae has been summarized elsewhere (6). The point to emphasize now is that the leaves of this family fall into three categories.

1. *Leaves with a sheathing base and a limb, more or less radial in form and phyllodic in anatomy.*—This form of leaf is rare in the family, but is found in the Sagittarias of the *S. teres* group, to which *S. isoetiformis* Smith and *S. teres* Watson belong. Fig. 1

[1] This paper represents part of the work carried out during the tenure of a Keddey Fletcher-Warr Studentship of the University of London.

represents a transverse section of the awl-like limb of one of these peculiar American Sagittarias. For comparison, by its side is a transverse section of the petiole of the normal arrowhead leaf of *S. sagittifolia* L. It will be recognized at once that both in form and structure they are essentially identical, and it will probably be generally agreed that the leaf of *S. teres* is equivalent to the arrowhead leaf of *S. sagittifolia*, minus the blade. DOMIN (9) evidently takes this view, for he uses the term "Phyllodien" in describing these leaves.

2. *Leaves with a sheathing base and a flat ribbon-like limb.*—These leaves are exceedingly common in the family, and are regarded as equivalent in morphological value to type 1, since in *S. sagittifolia* intermediate forms can be traced between thin ribbon leaves with a single row of bundles (fig. 3) and the almost radial petioles of the arrowhead type (fig. 2). For instance, among the transitional leaves between the juvenile ribbon and the mature arrowhead, a leaf was examined which was ribbon-like, but with a spathulate apex. It was found that the ribbon region was thicker than in the simple ribbon leaf, and, instead of having one series of bundles only, it had one small additional bundle above and one below the median bundle, and one below each of the main laterals, that above the median bundle being inverted. This showed an approach to the radial structure of the *S. teres* group.

3. *Leaves with a differentiated pseudo-lamina.*—I have set forth elsewhere (1) the reasons for regarding the blade of such leaves as the arrowhead as "pseudo-laminae," produced by the expansion of the distal part of the petiolar phyllode. How far the form and venation of the blades of the Alismaceae harmonize with this interpretation may now be considered. In some of the oval or cordate leaf forms there is little difficulty in seeing how the skeleton of the blade might be produced merely by the separation of the parallel petiolar veins, which at the apex return to their original approximation. This is the case, for instance, in *Alisma parnassiolium* Bassi var. *majus* (fig. 6). A further development on the same lines has taken place in *A. nymphaeifolium* Griseb. (fig. 8), in which the veins v and v', curving into the basal lobes, give off second-

ary veins, more or less parallel to themselves, and thus, without any essentially fresh departure, achieve a venation determining the auricled form of the leaf. It is probable, however, that such leaves do not form a transition to the arrowhead type, but that the latter is arrived at by a separate route.

It will be seen on examining fig. 5 (*Limnophyton obtusifolium*) and fig. 9 (*Sagittaria Greggii*) that the principal veins are the midrib (*a*) and the two veins (*b*, *b′*) passing into the cusps. In some species these cusps are very conspicuous; in *S. longiloba* they may be two or three times the length of the median segment. It is not probable that the arrowhead type of venation is derivable from that shown in fig. 8, which is, moreover, a rarity in the family. It is suggested that the veins *b* and *b′* are, as it were, a repetition of the midrib, and have originated phylogenetically by its chorisis. Their morphological relation to the midrib would thus be equivalent to the relation borne by the tendrils of *Smilax* to the petiole, according to a hypothesis put forward in a previous paper in this journal (**4**). Of course it is impossible to offer any definite proof of such a theory, but it probably makes the nature of the arrowhead leaf a shade less obscure. It seems to account for the lack of any genuinely transitional forms between the types of venation characterizing the oval and arrowhead varieties of pseudo-lamina. It is true that the intermediate forms have very short cusps, but their venation is distinctly of the arrowhead type.

Butomaceae

The Butomaceae are so closely related to the Alismaceae that they are sometimes regarded merely as a tribe of the latter family. Among the Butomaceae we find examples of the three types of leaf enumerated under the Alismaceae. *Butomus umbellatus* L. has a leaf with a sheathing base, and an upper region which is triangular in section and phyllodic in anatomy (**17**). On the other hand, *Hydrocleis Commersonii* Rich. and *H. parviflora* Seub. have both ribbon leaves and leaves with a petiole and pseudolamina (**10**, **18**, **20**). The published figures of these ribbon leaves suggest that they are equivalent to the ribbon leaves of *Sagittaria*, but I have not had the opportunity of examining their anatomy.

Juncaginaceae

Of the five genera of Juncaginaceae, none possesses leaves with pseudo-laminae. Certain species of *Triglochin* have ribbon-like leaves, for example, *T. montevidense* Spreng., figured by SEUBERT (18, pl. XII), and *T. procerum* R.Br. It is hoped to deal with the leaf anatomy of this genus in a later paper. Except in the case of these few ribbon-leaved species, all the five genera have leaves with a sheathing base and a radial or ensiform limb, with a typically phyllodic anatomy. In *Triglochin*, *Lilaea*, and *Scheuchzeria*, a ligule generally marks the boundary between sheath and limb (9). Fig. 7 shows the transverse section of the limb of the leaf of *Scheuchzeria palustris* L. Its curious asymmetry has been figured and commented on by RAUNKIAER (15). The leaf of the monotypic *Maundia*, judging from BUCHENAU'S figure of the transverse section (8, fig. 7, p. xvi), is phyllodic, and similar to that of *Triglochin maritimum* (1). I have cut the leaf of the monotypic *Lilaea subulata* Humb. et Bonpl., and, although the herbarium material available was not very favorable for anatomical work, it was obvious that here also the structure is phyllodic. The leaf, which is described as awl-shaped and cylindrical in the fresh condition, is supplied by a series of small peripheral bundles in addition to three main strands. HIERONYMUS (11), in a Spanish monograph of *Lilaea* published forty years ago, definitely states that the leaves of this plant consist only of sheath and petiole, the lamina being unrepresented.

It was interesting to find, on examining the fifth genus (the monotypic *Tetroncium magellanicum* Willd.) that the leaf is unusual among the Helobieae in being of the ensiform type, and in having a bundle system identical with that of the isobilateral equitant leaves which are so familiar, for instance, in *Iris*. In fig. 4, *A* shows the structure of the sheath region, *B* the transition to the limb, and *C* the limb itself, which has a close anatomical resemblance to that of *Tofieldia calyculata* Wahl., one of the equitant members of the Liliaceae (1). Fibrous sheaths are associated with the bundles.

Potamogetonaceae

In this family there are three types of leaf, corresponding to those met with in the Alismaceae and Butomaceae. The rarest type is the leaf with a sheathing base and more or less radial limb with phyllodic anatomy. This leaf form is found in *Cymodocea isoetifolia* Aschers. (fig. 11), described by SAUVAGEAU (16) and OSTENFELD (14). A ring of bundles surrounds the median strand. The same genus also includes leaves in which the limb is flat and furnished with only one series of bundles (as *C. nodosa* Aschers., fig. 12), while *C. manatorum* Aschers. (fig. 10), with its more or less terete leaf, traversed by three strands only, forms an intermediate type. In each species there is a ligule, clearly delimiting the sheath from the petiolar region.

In *Potamogeton* the leaves of some species, like the air leaves of many Alismaceae, possess pseudo-laminae. In *P. natans* L. there are, in addition, bladeless, terete, phyllodic leaves, corresponding exactly in structure and anatomy to the petioles of the fully developed leaves (16), and which may be regarded as equivalent to the leaves of *Cymodocea isoetifolia*. *P. natans* also has leaves showing a further degree of reduction, but instead of being ribbon-like, as in the Alismaceae, they consist almost entirely of the highly developed axillary stipules or ligules.

Naiadaceae

The leaves of the Naiadaceae are much reduced, but they have a sheath and a thin flat limb, and thus correspond to the ribbon leaves of *Sagittaria*.

Aponogetonaceae

Only the one genus, *Aponogeton*, is included in the Aponogetonaceae. Most of the species have leaves with a differentiated sheath, petiole, and pseudo-lamina, but *A. vallisnerioides* Bak. has ligulate ribbon leaves, described (7) as resembling those of *Vallisneria*, while in *A. spathaceum* E. Mey. var. *junceum* Hook. f. (12) semiterete leaves with a sheathing base are found. A piece of a leaf of this variety which was examined did not include the distal part of the leaf, but showed the structure of the transition region between sheath and limb. In addition to the three main bundles, which HOOKER indicates in a slightly magnified transverse section which he figures, there are a number of small peripheral bundles. The structure is thus closely equivalent to that of the petiole of such a species as *Aponogeton distachyum* Thunb.

Hydrocharitaceae

In the Hydrocharitaceae all three types of leaf which have been considered are found. In *Stratiotes* and *Enhalus* there is no blade, and the occurrence of inverted bundles (13, 19) gives a phyllodic aspect to the anatomy. These leaves may be regarded as equivalent to that of *Butomus*, but in *Stratiotes* there is no sheath, although this region is developed in *Enhalus*. *Hydrocharis* has a leaf with a stipulate sheath, a petiole, and a pseudo-lamina, while the leaves of *Vallisneria* and *Thalassia* are similar to the ribbon leaves of *Sagittaria*. *Vallisneria* has a sheath which may easily be overlooked, while in *Elodea* this region is entirely lacking (9).

Conclusions

A comparison of the leaf structure in the various families belonging to the Helobieae shows the repeated occurrence of that leaf type in which there is a sheathing base succeeded by a bladeless limb, in appearance and structure recalling a petiole. Such leaves, instances of which are met with in six of the seven families, are regarded as *typical petiolar phyllodes*. This simple phyllodic form of leaf is most characteristically developed in the Juncaginaceae, where it occurs in all five genera. The leaves in this family are generally more or less radial, except in *Tetroncium*, where they are ensiform and *Iris*-like. In the other families leaves of approximately radial structure occur more or less sporadically, or as rarities, except in the Naiadaceae, where they are entirely lacking. The extreme reduction of the one genus *Naias*, which constitutes the family, however, makes the absence of such leaves by no means surprising.

In each of the seven families examples of a leaf with a sheathing base and flat ribbon-like limb are found. This leaf is regarded as equivalent to the more obviously phyllodic type of leaf just discussed. Two lines of evidence point to this conclusion: (1) within the single species *Sagittaria sagittifolia* L. transitions, both in external form and internal structure, can be found between typical ribbon leaves and petioles; and (2) within *Cymodocea* not only typical ribbon leaves (as *C. nodosa*, fig. 12) and typical petiolar leaves (as *C. isoetifolia*, fig. 11) are found, but also in *C. manatorum* (fig. 10) there is an intermediate link between these two types.

The third and last leaf type, that in which there is a differentiated blade, occurs in five of the seven families, the exceptions being the Juncaginaceae and Naiadaceae. It is not necessary here to discuss the evidence, based partly on a study of the succession of leaf forms in the ontogeny, and partly anatomical, which has led to the conclusion that these blades are "pseudo-laminae," originating by the expansion of the apex of the petiolar phyllode, for this question has been considered elsewhere (**1**, **6**). The present paper adds a study of the significance of the blade venation of the Alismaceae.

The final impression left by this survey of the leaves of the Helobieae is that there has been a remarkable parallelism of development within the different families. The three leaf types enumerated recur throughout the cohort in forms which, although modified in various ways, are identical in essentials.

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LITERATURE CITED

1. ARBER, AGNES, The phyllode theory of the monocotyledonous leaf, with special reference to anatomical evidence. Ann. Botany **32**: 465–501. 1918.
2. ———, The vegetative morphology of *Pistia* and the Lemnaceae. Proc. Roy. Soc. B. **91**:96–103. 1919.
3. ———, Leaf base phyllodes among the Liliaceae. BOT. GAZ. **69**:337–340. 1920.
4. ———, Tendrils of *Smilax*. BOT. GAZ. **69**:438–442. *pl. 22*. 1920.
5. ———, On the leaf structure of certain Liliaceae, considered in relation to the phyllode theory. Ann. Botany **34**:447–465. 1920.
6. ———, Water plants: a study of aquatic Angiosperms. Cambridge University Press. 1920.
7. BAKER, J. G., and GRANT, J. A., The botany of the Speke and Grant expedition. Trans. Linn. Soc. **29**:1–190. 1875.
8. BUCHENAU, F., Scheuchzeriaceae in Das Pflanzenreich IV. **14**:1–20. 1903.
9. DOMIN, K., Morphologische und phylogenetische Studien über die Stipularbildungen. Ann. Jard. Bot. Buit. **24**:117–326. *pls. 11*. 1911.
10. ERNST, A., Über Stufengang und Entwickelung der Blätter von *Hydrocleis nymphoides* Buchenau (*Limnocharis Humboldtii* C. L. Richard). Bot. Zeit. **30**:518–520. 1872.
11. HIERONYMUS, G., Monografía de *Lilaea subulata*. Act. Acad. Nac. Ciencias en Córdoba. **4**:1–52. *pls. 5*. 1882.
12. HOOKER, J. D., *Aponogeton spathaceum* E. Mey. var. *junceum*. Curtis's Bot. Mag. **34**: *pl. 6399*. 1878.

13. MAGNUS, P., Über die Anatomie der Meeresphanerogamen. Sitz.-Ber. Gesells. Nat. Freunde Berlin 1870. 85–90.

14. OSTENFELD, C. H., Contributions to West Australian botany. Part I. Introduction. The sea-grasses of West Australia. Dansk Bot. Arkiv 2:1–44. 1916.

15. RAUNKIAER, C., De Danske Blomsterplanters Naturhistorie. I. Enkimbladede, 1. Helobieae. 1–138. Copenhagen. 1896.

16. SAUVAGEAU, C., Sur les feuilles de quelques monocotylédones aquatiques. Ann. Sci. Nat. VII. Bot. 13:103–296. 1891.

17. ———, Sur la feuille des Butomées. Ann. Sci. Nat. VII. Bot. 17:295–326. 1893.

18. SEUBERT, M., in MARTIUS, Flora Brasiliensis 3: part 1. 1842–71.

19. SOLEREDER, H., Systematisch-anatomische Untersuchung des Blattes der Hydrocharitaceen. Beih. Bot. Centralbl. 30:24–104. 1913.

20. WÄCHTER, W., Beiträge zur Kenntniss einiger Wasserpflanzen. Flora 83:367–397. 1897.

EXPLANATION OF PLATE I

The plate shows the xylem in black, the phloem in white, the fibers (*f*) dotted, and the outlines of lacunae in dotted lines.

FIG. 1.—*Sagittaria* of *S. teres* group: transverse section of limb of leaf *f*, interrupted fibrous sheath of bundle (slight asymmetry of section probably due to incomplete recovery of herbarium material used; Georgia Plants. Roland Harper. 1473. Ex Herb. Brit. Mus.); ×23.

FIG. 2.—*Sagittaria sagittifolia* L.: transverse section of petiole close to blade, fibrous bundle sheath (less highly developed than in species shown in fig. 1) not indicated; ×14.

FIG. 3.—*Sagittaria sagittifolia* L.: transverse section of small ribbon leaf, ×23.

FIG. 4.—*Tetroncium magellanicum* Willd.: transverse sections of leaf; *A*, sheath, *B*, transition to limb; *C*, limb; ×23.

FIG. 5.—*Limnophyton obtusifolium* Miq.: blade of leaf; *a*, midrib; *b*, *b'* cusp veins (serration of margin probably an effect of drying); ×0.5.

FIG. 6.—*Alisma parnassifolium* Bassi var. *majus*, blade of leaf; ×0.5.

FIG. 7.—*Scheuchzeria palustris* L.: transverse section of limb of leaf; *f*, fibrous strand occupying one margin (on account of small scale, fibrous sheaths of bundles not separately indicated); ×23.

FIG. 8.—*Alisma nymphaeifolium* Griseb.: blade of leaf; *v*, *v'*, principal veins of auricles; ×0.5.

FIG. 9.—*Sagittaria Greggii* Smith.: blade of leaf; *a*, midrib; *b*, *b'*, cusp veins; ×0.5.

FIG. 10.—*Cymodocea manatorum* Aschers.: transverse section of limb of leaf; ×23.

FIG. 11.—*Cymodocea isoetifolia* Aschers.: transverse section of limb of leaf; xylem indistinguishable, in smaller bundles surrounding median bundle; ×23.

FIG. 12.—*Cymodocea nodosa* Aschers.: transverse section of limb of leaf; ×23.